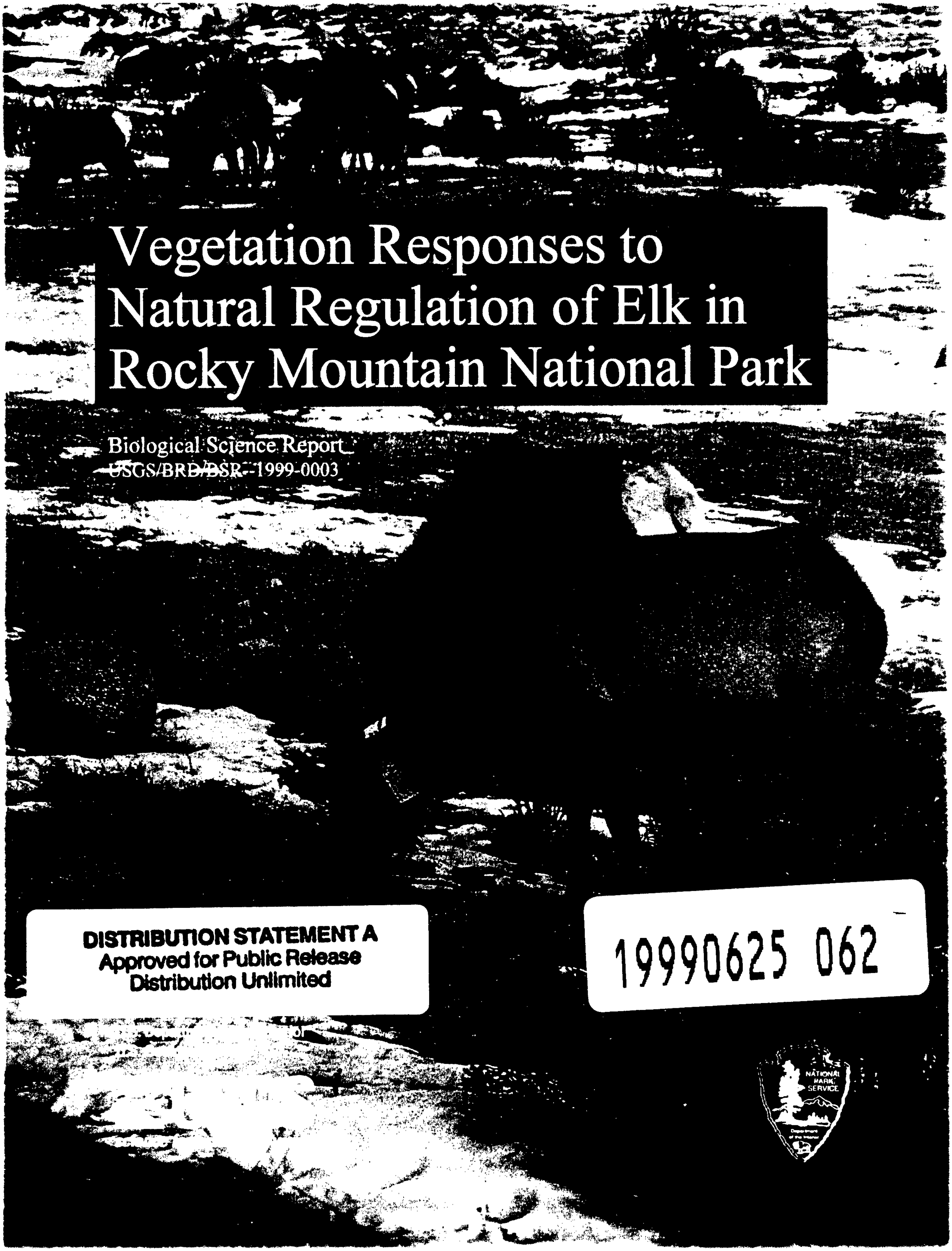
Vegetation Responses to Natural Regulation of Elk in Rocky Mountain National Park

Biological Science Report
USGS/BRD/BSR--1999-0003



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May 1999

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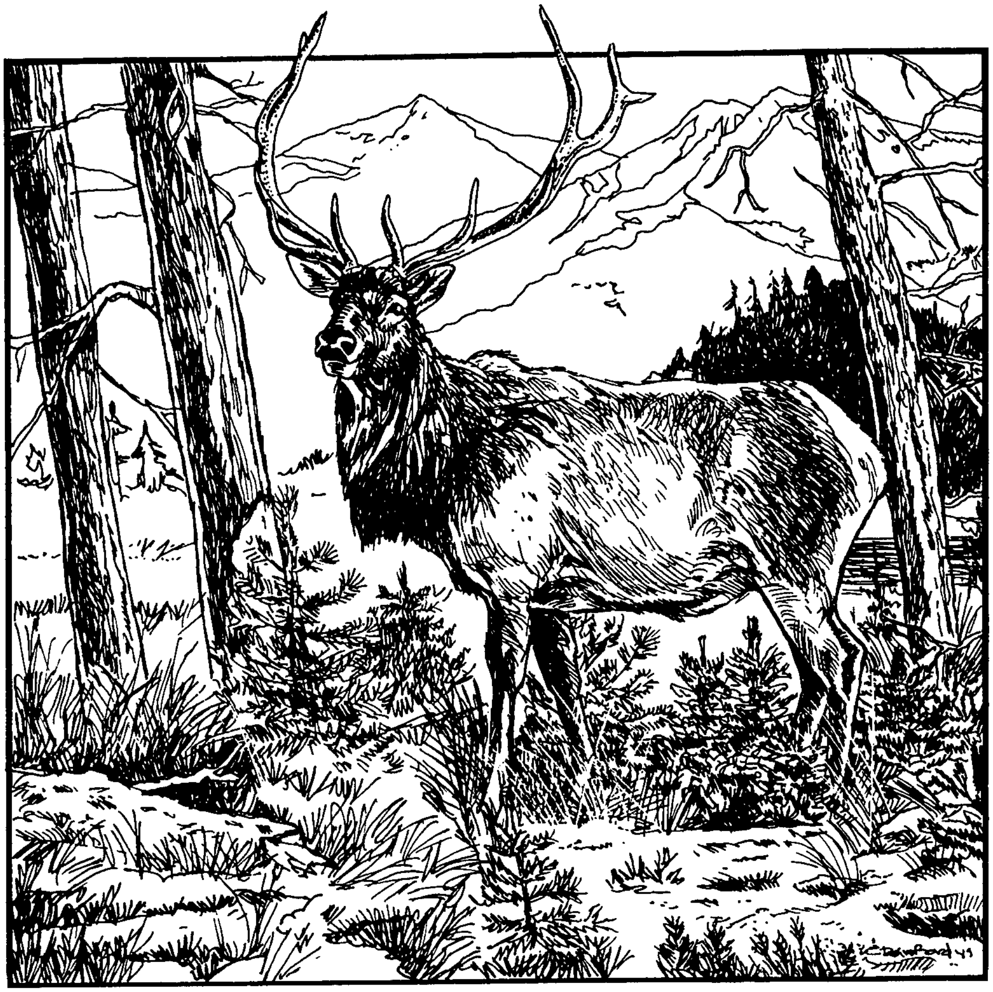

Vegetation Responses to Natural Regulation of Elk in Rocky Mountain National Park

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Abstract. Little experimental information is available on the relationship between herbivory by native ungulates and vegetation in relatively undisturbed environments. A quasi-experimental situation exists in Rocky Mountain National Park, where elk (*Cervus elaphus*) populations have increased about 3-fold since 1968, following their release from artificial controls within the park boundaries. We reviewed data collected on vegetation transects established and monitored over the 25-year period from 1968 through 1992. Data were subjected to rigorous statistical analysis to detect trends following the release of elk from artificial controls. Increases in elk habitat use and decreases in deer habitat use were observed on all transects over the 25-year period. Significant increases in moss and lichen cover occurred in three of four vegetation types. Percent cover of bare ground, forbs (particularly *Selaginella densa*), and *Carex* spp. increased on grassland transects. Increases in timothy (*Phleum pratense*) were observed on meadow transects. Graminoid and litter cover increased on sagebrush transects, and shrub and litter cover increased on bitterbrush transects.

We concluded the lack of control (fenced) plots in this sampling design, the types of measures, the small number of replicates, and nonrandom placement of plots limit the inferences and sensitivity from the work. Unique strengths of the work included the long time period (25 years), good distribution of samples, consistency of the observer (D. Stevens), and placement of the plots in the most heavily grazed sites.

Some grazing-induced responses were detected. Grazing-resistant species such as sedges (native), timothy (exotic), and club mosses increased and the amount of bare ground increased on some grazed sites. However, the changes within this sampling program alone were not alarming. The amount of bare ground increase was minor (4%), and grass and shrub cover increased in the shrub plots. The inferential power of this sample design was limited to the study plots only. Other factors (climate change, succession) were not controlled for using fenced plots and the sensitivity of the methods and plots to detect change were limited. For example, the low number of transects in willow was not adequate to monitor conditions on the entire winter range. Lacking controls, observed changes may have been due to other factors (climate trends, beaver dam abandonment, stream channel changes), not elk herbivory alone. We recommend using a new sampling design that would include controls, pretreatment data, random site selection, and much more replication.

Key words: elk, herbivory, natural regulation, potential overgrazing, vegetation monitoring.

Introduction

Little experimental information is available on the relationship between herbivory by native ungulates and vegetation in relatively undisturbed environments. A quasi-experimental situation exists in Rocky Mountain National Park, where elk (*Cervus elaphus*) populations have increased about 3-fold since 1968, following their release from artificial controls within the park boundaries. Elk were native in the area, but were extirpated, or nearly so, by the late 1800's. Elk were reintroduced to the area in 1913–1914, and steadily increased until they numbered about 1,000 in 1944 (Packard 1947), but due to concerns over vegetation conditions, populations were reduced and then held below 500 from that time until 1968. Culling of the herd was discontinued in 1969 under the premise that elk within the park would regulate themselves if left alone, and following release from artificial controls, they subsequently increased. Ambitious efforts were made by the agencies involved to slow or control the elk densities on lands immediately outside the park through late season harvests of both sexes. Interagency goals were to harvest 500–600 elk per year, a number that was 15% to 17% of the estimated elk population — a level of harvest that might have limited or regulated the elk population, depending on the rate of other elk losses. The maximum rate of increase in a wild elk population where survival rates are high is about 33% per annum (Eberhardt et al. 1996). But it has proven impossible to obtain a harvest of 500–600 elk, and more recently, access to private lands and tolerance for sport hunting have declined in the area. Human developments such as subdivisions, town developments, and ranchettes with a few head of horses, have increased exponentially in the past 10–15 years. The human population of the Estes Valley in 1970 was 3,554. That number was projected to reach 10,595 by 1995 (U.S. Census Bureau data). As a result of less access by sportsmen to private lands, elk harvests declined from 442 ± 78 ($\bar{x} \pm$ SD) before 1987 to 302 ± 36 since 1987, raising concerns that the elk population has further increased since 1987 (Fig. 1). Elk have habituated to people and the developments in town, and as a result, have recently gained access to rich food sources in the form of irrigated and fertilized golf courses, pastures, lawns, and ornamental shrubs. Access to these new food sources, combined with shallow snows in town, might have further fueled the elk increases. Concerns over possible further elk increases since 1987 have been expressed by agency managers and others (Hess 1993).

Elk were absent or held to low densities by human controls on the winter range for over half the century (late 1800's to 1969) and vegetation conditions and succession may have changed as a result of the underpopulation of a large native herbivore. Some vegetation changes observed since 1969 might be interpreted as a return to more natural conditions with the return of elk to a more significant role in the ecosystem. Vegetation conditions may not be declining beyond natural conditions to be expected from elk grazing (Stevens 1980,1992; Houston 1982).

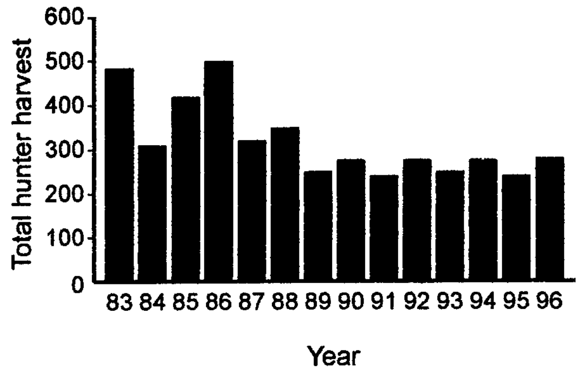


Fig. 1. Total hunter harvest of elk outside Rocky Mountain National Park from 1983–1994.

National parks have a mission to preserve natural ecosystems and processes (U.S. Department of the Interior, National Park Service 1988). Large native ungulate herbivores can influence many aspects of plant structure, growth, and net primary productivity. Ungulates grazing and the action of their hooves can result in more bare ground, soil compaction, and higher sediment yields from grazed sites. Increases in bare ground could result in a warmer or drier soil microclimate. A warmer soil, if moisture is equivalent, could result in increased nitrogen mineralization on grazed sites. Ungulates can also influence the nitrogen cycle by changing litter quality, thereby affecting nitrogen mineralization rates, and by adding readily available nitrogen to the upper soil levels in the form of urine and feces (Hobbs 1996). Thus, the natural heterogeneity of nitrogen within the landscape can be influenced by ungulates.

Net primary productivity can either increase or decrease as a result of ungulates. Elk grazing increases nitrogen and other nutrient content and digestibility of forages in other study areas (Frank and McNaughton 1992; Singer and Harter 1996). Elk apparently return nutrients to the grasslands at a high rate (Frank and McNaughton 1992) and grazed plants may be less susceptible to drought effects. Intensely grazed grasses and

shrubs had more optimal root:shoot ratios, longer growing seasons, higher water conductance, and higher survival than ungrazed counterparts (Georgiadis et al. 1989; Welker and Menke 1990). McNaughton (1979) and Holland and Detling (1991) observed that rates of photosynthesis and nitrogen uptake were higher on grazed sites. Ungulates can create spatial heterogeneity, modulate successional processes, and control the switching of ecosystems between alternative states (Hobbs 1996). Thus, we regard ungulate herbivory as a natural ecosystem process. Some effects of elk on vegetation, soil, and nutrient processes, whether positive or negative, should be considered normal and natural in a national park ecosystem where elk are a native species.

The challenge for land and resource managers is to determine what conditions are "natural" (a value-laden term) because so little information is available for the area prior to the influence of settlers in the mid-1800's. It is not clear at what point the effects of elk herbivory exceed those expected under natural conditions and become excessive effects, or overgrazing. National Park Service (NPS) policy states that ungulates in parks can be controlled when those concentrations are unnatural and due to the effects of modern man, but unnatural concentrations can also be hard to define operationally (U.S. Department of the Interior, National Park Service 1988). However, natural processes to control populations of native species should be relied upon to the greatest extent possible.

Definitions of Overgrazing

Overgrazing is also a value-laden term which can be defined in various ways (see review by Coughenour and Singer [1991]). Overgrazing is defined simply as any excess of herbivory that leads to degradation of plant and soil resources. The excess, which may be caused by humans, should be defined. By our definition, overgrazing could not occur in a pristine pre-Columbian ecosystem with intact predator fauna. Those grazing effects should all be considered natural and undisturbed.

One's perceptions might influence how overgrazing will be defined. A range manager might define overgrazing as any grazing in excess of that level which would result in maximum production of livestock animal tissues from the system. A wildlife manager might seek maximum sustained yield (MSY) for sport hunting purposes. In that context, overgrazing would be in excess of that for MSY. Typically, MSY for a wild herbivore like elk might be 53% to 60% of the ecological carrying capacity of the habitat (ECC or K). Ecological carrying capacity, or the ungulate-vegetation ceiling, is defined as the maximum dynamic capacity of the habitat, forage, and climate of the area to sustain the herbivore. Thus, if K of a certain area was estimated at 1,700 elk, MSY might occur at about 1,200 elk and any grazing in excess of that would be overgrazing. In the most liberal context, ungulates, whether native or nonnative, are predicted to obtain a new stable equilibrium with their vegetative forage base — the Caughley model (Caughley 1979, 1981). In the Caughley model, considerable mortality of some plants, major shifts in plant species to less palatable and more resistant species, and some reduction in plant productivity, are quite acceptable. Just let the animals and plants do their own thing and everything will be all right. That is what has happened time and time again in nature. For example, when elk and other ungulates crossed the Bering Land Bridge, they encountered systems that were not yet adapted to their herbivory and yet, eventually, the system adapted. Obviously, none of these definitions is appropriate for a national park.

Four hypothetical scenarios of elk density have been proposed for Yellowstone National Park, where this subject has been intensely investigated but where little agreement exists within the scientific community (Fig. 2). The first proposed density scenario, the natural regulation hypothesis of Cole (1971) and Houston (1971, 1976), predicts a food-limited elk density at or near ECC or K with little or no limitation by predators or Native Americans. This was the premise by which elk were released from artificial controls in both Yellowstone and Rocky Mountain National Parks in 1968. But in the ensuing decades it was determined that predators, especially where both bears and wolves were significant,

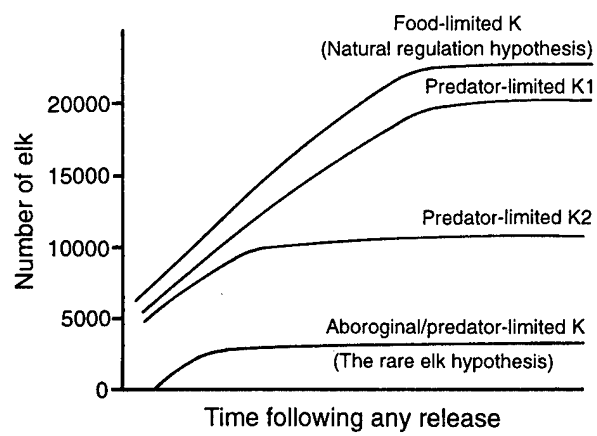


Fig. 2. Four hypothetical scenarios of elk density in Yellowstone National Park under different carrying capacity models (from Cole 1971; Boyce 1993; Lime et al. 1993; Kay 1994).

could limit, and possibly regulate, ungulates in many situations (Bergerud et al. 1983; Boutin 1992; Gasaway et al. 1992). The second proposed scenario, based on predictions and extensive computer simulations, suggests wolves and bears would reduce elk 8% to 20% following full restoration of 75–100 wolves to the northern area — the predator-limited K_1 of Garton et al. (1990), Boyce (1993), and Mack and Singer (1993). Third, based on observations from the far north, other wolf experts predict 200 wolves will occupy the area and wolves and bears will limit elk to 40% to 50% of K — the predator-limited K_2 (Gasaway et al. 1992; Lime et al. 1993; Messier 1995). The fourth scenario, the rare elk hypothesis, is based on the premise that Native Americans were efficient at hunting and pursued elk to great lengths and reduced elk populations to <10% of K (Kay 1990, 1994; Wagner et al. 1995a,b).

For purposes of this paper, we define overgrazing in three contexts. We suggest all three might be considerations in a management decision. First, appropriate grazing may be defined in terms of the population density of elk that are suspected to have occurred on the park winter ranges at the time of pre-Columbian man, with natural migrations of elk in place and intact native predator fauna.

This, our preferred choice for a population density definition of overgrazing, is that wolves, bears, and other predators limited elk numbers in prehistoric times in Rocky Mountain National Park to about one-fourth less than the K for the area. We selected this scenario based on the greater consensus of experts and modelers who preferred this option (Garton et al. 1990; Boyce 1993; Lime et al. 1993; Mack and Singer 1993). We hasten to add, however, that a high degree of uncertainty and scientific debate surround these predictions.

Secondly, we propose another definition of overgrazing for Rocky Mountain National Park based on plant mortality, species composition, alterations to less palatable plants, or alterations to ecosystem processes beyond those effects expected from the system prior to arrival of modern man. There should be no reduction in plant cover, no increase in bare ground, no reduced input of organic matter, no increase in soil temperature or decrease in soil moisture, nor any increase in sediment or nutrient loss beyond levels expected from elk in a natural, undisturbed ecosystem. In other words, the effects of grazing of elk that occurred in prehistoric times with an intact native predator guild should be acceptable and grazing effects beyond that level should be unacceptable.

A third definition of overgrazing is any grazing beyond that level of elk grazing that is sustainable over long periods of time. In other words, there should not be a net loss of nitrogen, organic matter, or other nutrients of a magnitude that would not be sustainable over a long period of time. Elk herbivory in excess of that level would be overgrazing.

The objectives of this report are to review, analyze, and interpret the data collected on vegetation transects and plots established and monitored by former park biologist D. Stevens, from 1968, following the release of elk from artificial controls, to 1992. We subjected the data to statistical analysis to detect trends following the release of elk. We also comment on whether this sampling design is sensitive enough to detect changes on this range from 1968–1992 and we provide recommendations on improved experimental and sampling designs that are more robust.

Description of the Study Area and Elk Populations

Study Area

Description of the study area was taken from Gysel (1959), Stevens (1980), and Hobbs et al. (1981). The elk winter range on the east side of Rocky Mountain National Park encompasses about 8,000 ha on the eastern slope of the Continental Divide in the upper montane zone. Glacial moraines running east-west divide the body of this area into four major valleys: Horseshoe Park, Beaver Meadows, Moraine Park, and Hallowell Park. Elevations in the study area range from 2,400 m at the valley bottoms to 2,800 m on moraine ridgetops. Mean annual precipitation is 41 cm, most occurring as wet spring snows. North-facing slopes are dominated by dense stands of lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*), while communities of ponderosa pine (*Pinus ponderosa)*/shrub (mainly *Purshia tridentata*) and big sagebrush (*Artemisia tridentata*) dominate south-facing slopes. The flat valley bottoms are covered with sedges (*Carex* spp.), grasses, and riparian shrubs (*Salix* spp., *Betula* spp.) in wetter areas, and grasses in drier areas.

Predominant vegetation types in the upper montane zone include ponderosa pine/shrub, ponderosa pine/Douglas fir, lodgepole pine, mesic montane forest, aspen (*Populus tremuloides*), willow, shrub/grassland, grassland, meadow, and wet meadow. Elk typically utilize the conifer forests mainly for resting during midday and move into meadows and grasslands in the morning and evening to feed (Stevens 1980; Green and Bear 1990). While the winter range extends beyond the park boundaries into the town and valley of Estes Park, this study was primarily limited to the areas within Rocky Mountain National Park (Fig. 3).

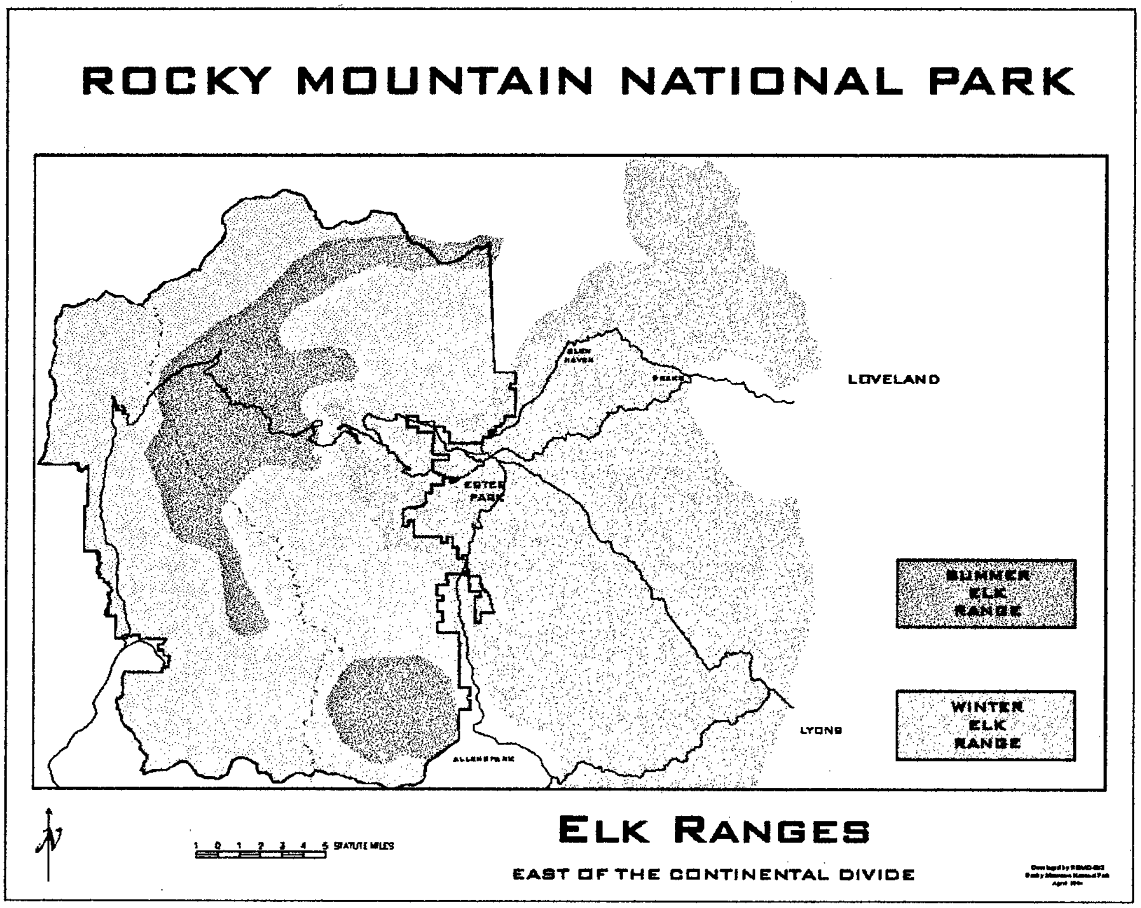


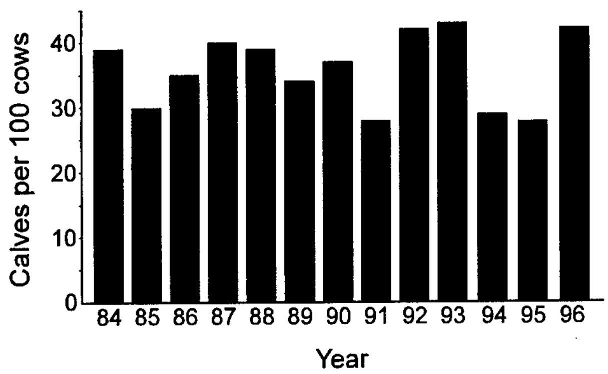
Fig. 3. Winter and summer elk ranges east of the Continental Divide in Rocky Mountain National Park.

Elk Populations

Our analysis of elk use of plants and vegetation trends would be incomplete without concurrent knowledge on elk population densities. At the time elk were released from artificial controls in 1968, park managers estimated 500 elk occurred within the park (Stevens 1980, 1982). Some uncertainty surrounds this figure since it was based on ground counts. But the estimate was generated by biologist, Neil Guse, who knew the elk population and winter range well. Elk could be found and were regularly hunted outside of the park from 1942 to 1968, but at the time of the release of the park elk from controls, few elk inhabited the town of Estes Park (T. Hobbs, personal communication.). Following cessation of controls within the park, elk increased rapidly and in 1979–1982, Bear (1989) estimated there were 2,273 (range 1,627 to 3,075) elk in the entire (park and Estes Valley) population. Unfortunately, Bear (1989) did not report a separate estimate for the park alone, but it appears that elk increased 2- to 3-fold in the park. Additionally during this period, elk began to habituate to, and use, the town area more, where they gained access to rich food sources in irrigated and fertilized pastures and lawns. The town of Estes Park is approximately 250 m lower in elevation than park winter ranges, snow depths are shallower, and temperatures are warmer. Between 1968 and the present, elk increasingly invaded and took advantage of an unoccupied, but fertile, habitat in the town.

Calf/cow ratios (calves/100 cows) gathered in the area also provided evidence that elk were increasing after 1968. Calf/cow ratios averaged 48 ± 7 from 1979–1982, suggestive of an elk increase, but calf ratios declined to 36 ± 8 from 1991–1996, suggestive of a slowing of the elk increase (Fig. 4). Calf/cow ratios were also higher in the town than the park during 1990–1996, suggesting the rate of elk increase, at least in recent years, was higher in town.

a)



b)

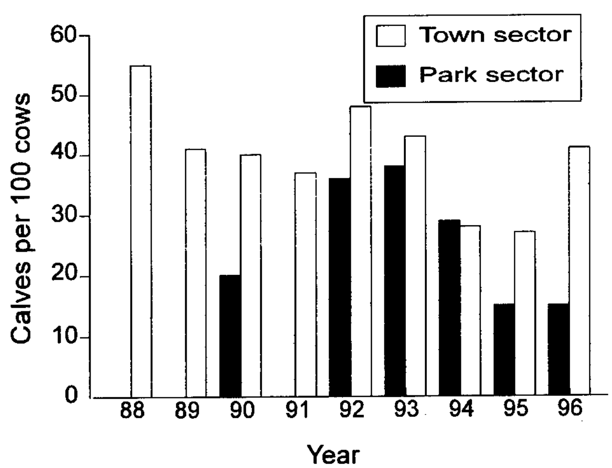


Fig. 4. Ratio of calves/100 cows on Rocky Mountain National Park winter range, 1984–1996 (a); and compared between the park (aerial classification) and town (ground classification), 1988–1996 (b).

Methods

Vegetation Trends

In 1968, then park biologist David Stevens, established a long-term monitoring program in key vegetation types used by elk. He selected representative sites in those vegetation communities and locales receiving the highest elk use (Stevens 1980, 1992). Transects were chosen nonrandomly and were well-distributed across the winter range in easily accessible areas of highest elk densities. Transects were not established in peripheral or low-use areas of the winter range.

Forty-two line transects were established in six key vegetation types on the elk winter range of Rocky Mountain National Park from 1968–1971 (Fig. 5). Primary transect lines were 100 ft (30.49 m) in length and established along the contour. Nine of these transects were in bitterbrush (*Purshia tridentata*); 4 in sagebrush (*A. tridentata*); 4 in aspen (*Populus tremuloides*); 6 in willow (*Salix* spp.); 8 in meadow; and 11 in upland grasslands. Elk diets on the eastern winter range of Rocky Mountain National Park consisted of a wide variety of species, mainly graminoids, 55%, followed by shrubs, 38%, and forbs, 6% (Table 1) (Stevens 1980; Hobbs et al. 1982).

Elk Use

Transects in bitterbrush, sagebrush, willow, and aspen were established to monitor browsing by elk and deer on the major shrub species on these transects. On each of these transects, 25 to 40 shrubs of the key species for that vegetation type were tagged along the transect line and assessed annually for percent leader use, form class, and decadence following the "key browse technique" of Cole (1963). Data on average height and percent cover of shrub species were collected approximately once every 5 years using the line intercept method (Canfield 1941), on bitterbrush, sagebrush, and willow transects. Data on height, basal area, and density were collected approximately once every 5 years using the point-centered quarter method (Phillips 1959; Mueller-Dombois and Ellenberg 1974), on aspen transects.

Plant utilization and use of the transects by elk and deer were measured annually on grassland and meadow transects. A variety of methods were used throughout the 25-year period to determine percent utilization on these transects, including clip-and-weigh, counts of grazed versus ungrazed plants, and ocular estimation. Use by deer and elk was monitored annually by counting the number of pellet groups of each species on 10 100-ft^2 (9.3 m^2) plots, located on a line parallel to the primary transect line, on all transects, except those in willow. Days use per acre by deer and elk were calculated following the methods described by Overton and Davis (1969), using the formula:

$$t = \frac{(1/a)\sum y_i}{13}$$

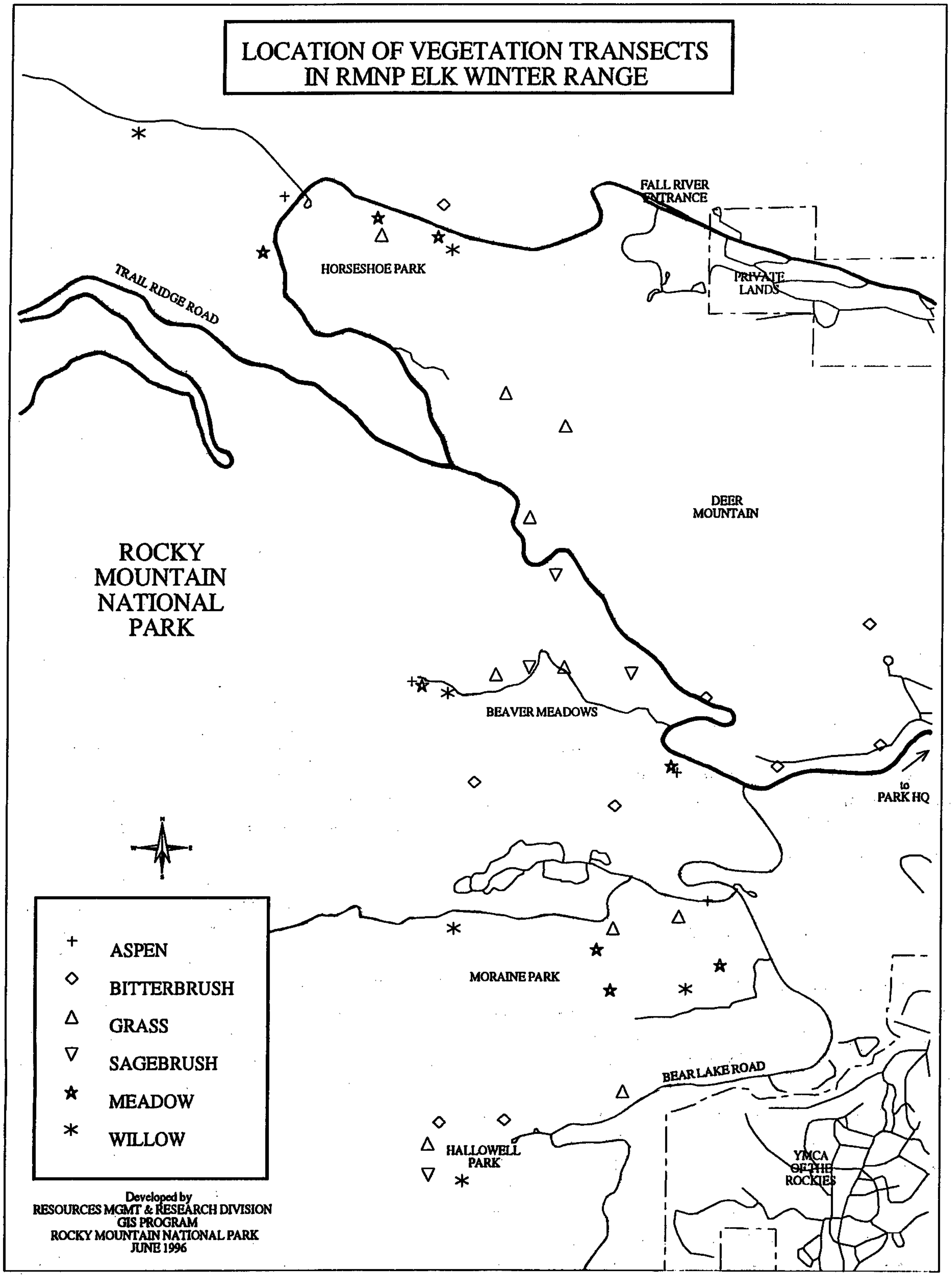


Fig. 5. Location of vegetation transects on Rocky Mountain National Park elk winter range used by D. Stevens from 1968–1992.

Table 1. Predominant components of elk winter diets in Rocky Mountain National Park from Hobbs et al. (1982) and Stevens (1980).

Graminoids	Forbs	Shrubs
Bromus inermis	*Eriogonum umbellatum*	*Salix* spp.
Bouteloua gracilis	*Potentilla* spp.	*Populus tremuloides*
Calamagrostis canadensis		*Purshia tridentata*
Carex spp.		*Potentilla fruticosa*
Juncus balticus		*Rosa woodsii*
Muhlenbergia montana		*Alnus tenuifolia*
Muhlenbergia richardsoni		*Prunus virginiana*
Phleum pratense		*Chrysothamnus viscidiflorus*
Stipa comata		*Betula* spp.
Poa spp.		*Ribes* spp.

where t = days of use per acre by deer or elk, a = the total area sampled (in acres), and y_i = the total number of pellet groups per acre on the ith sample plot. A defecation rate of 13 groups per day was assumed for both deer and elk, thus:

$$43.55\sum y_i/13 = 3.35\sum y_i,$$

which is days use per acre we used.

A modified Daubenmire (1959) technique was used to determine occurrence and percent cover of herbaceous and small shrub species on bitterbrush, sagebrush, grassland, and meadow transects. These samples were collected approximately once every 5 years. This technique involved sampling 21 (20 x 50 cm) plots distributed at 5 ft (1.52 m) intervals along the 100 ft (30.5 m) transect line.

Statistical Methods

Both parametric and nonparametric methods of analysis were used. Because transect locations were subjectively selected, transects were treated as fixed effects using two-way analysis of variance with year as the other factor. Linear contrast methods were used to test for significant trends in the responses over time. Nonparametric analyses (rank transformations) were used for variables which otherwise might violate the distributional assumptions required for analysis of variance procedures (parametric analyses). In the nonparametric analysis, the data were ranked by transect, and then ranked data were analyzed using general linear models. Annual data were analyzed using general linear models (PROC GLM) to determine significant changes over the 25-year period in average percent leader use, average days of elk use per acre, and average days of deer use per acre year. Percent cover by species, height, density, and basal area data, from the Daubenmire, line intercept, and point-centered quarter plots were analyzed using PROC GLM and ranked by species. Percent change in variables which is reported in the **Results** section is based on regression models fitted to the data. Analyses were performed using SAS 6.08 statistical software.

We did not analyze utilization data from grassland and meadow transects because variation in sampling methods through the years may have affected the comparability of the data from one sampling period to the next. We performed no statistical analyses on decadence and form class data on browse transects due to the subjective and qualitative nature of these data, and because tag numbers were often reused when the original tagged plant died.

The entire data set for each vegetation type was broken into smaller subsets for analysis in those instances where the first sampling year differed among the transects. When significant trends over time were observed in all subsets for a vegetation type, we assumed that the trend was significant for the vegetation type as a whole. One willow transect and one aspen transect were dropped from the 25-year analysis because the original transects were destroyed in 1982 by the Lawn Lake flood.

Results

Trends in Elk Habitat Use

Increases in elk habitat use and declines in deer habitat use, as evidenced by pellet counts over the 25-year period, were observed on all transects which had pellet counts. There was no overall change in consumption (percent leader use) of browse species.

Changes in cover of graminoids, forbs, shrubs, mosses/lichens, litter, and bare ground varied by vegetation type (Table 2). Significant (P <0.05) trends are summarized by vegetation type below.

Grassland Transects

Elk habitat use, as indicated by density of fecal piles, on grassland transects increased by 48% over the period 1969–1993 (Fig. 6a). Deer habitat use, however, decreased from the period 1969–1984 and then increased from 1985–1993 (Fig. 6b). Overall, deer habitat use decreased by 48% on these transects over the entire sampling period. Significant increases in percent cover of bare ground (34%), forbs (30%), and lichens/mosses (1,200%) on these transects occurred from 1968–1988 (Fig. 7a,b,c). Most of the increase in forbs is attributable to the increase of *Selaginella densa*. Percent cover of *Carex* spp. more than doubled (136% increase). Little clubmoss (*S. densa*) and lichen species increased significantly (76% and 728%, respectively) throughout this period as well (Fig. 8a,b,c).

Meadow Transects

Elk habitat use on meadow transects doubled over the period 1971–1992 (Fig. 9). Percent cover of *Phleum pratense* showed a significant increase of 54% over the period 1978–1988 (Fig. 10).

Aspen Transects

No significant changes were found in basal area, density, or average height of aspen trees on these transects for the period 1968–1988. But the variance between transects was large and the number of sample plots (n = 3–4) was small.

Willow Transects

Ungulate herbivory, documented by percent leader use on willow transects, did not change substantially during the period 1968–1992. There are indications of a slight decline from 1968–1983 (9%), followed by an increase (3%) through 1992 (Fig. 11). Overall, percent leader use declined by 6% from 1968–1992. Mean height of *Alnus tenufolia* increased 78% from 1973–1988 (Fig. 12).

Sagebrush Transects

No significant changes in consumption (percent leader use) on sagebrush transects occurred during the period 1968–1992. Elk habitat use (days use per acre) increased 112% on these transects throughout the period between 1968–1992 (Fig. 13a). Deer days use per acre declined from 1968–1983, then increased during 1984–1992 (Fig. 13b). Overall, deer use declined 48.7% over the entire period. Ranked data for mean height of *Purshia tridentata* showed a significant increase over the period 1968–1988. Mean height (unranked data) increased 56% over this period (Fig. 14). Percent cover of grasses, mosses/lichens, and litter increased by 32%, 1063%, and 62% respectively, on sagebrush transects between 1968–1988 (Fig. 15a,b,c).

Bitterbrush Transects

No significant trend in consumption (percent leader use) was apparent on bitterbrush transects from 1969–1992. Elk days use per acre increased 62% on bitterbrush transects from 1969–1992 (Fig. 16a). Deer days use per

Table 2. Statistically significant change of measured variables (P <0.05) over 25-year period 1968–1992 (0 = no change, + = increase, – = decrease).

Vegetation type	Days use per acre		Percent leader use of shrubs	Percent cover by functional group					
	Elk	Deer		Graminoids	Forbs	Shrubs	Mosses/ lichens	Litter	Bare ground
Grassland	+	–		0	+	0	+	0	+
Meadow	+	0		0	0	0	0	0	0
Willow			0						
Aspen			0						
Sagebrush	+	–	0	+	0	0	+	+	0
Bitterbrush	+	–	0	0	0	+	+	+	0

acre decreased 63.6% over this same period (Fig. 16b). Percent cover and mean height of *P. tridentata* increased, 36% and 14%, respectively, on bitterbrush transects over the period 1968–1988 (Fig. 17a,b). Percent cover of mosses/lichens, litter, and shrubs increased 123%, 50%, and 24%, respectively, over this period (Fig. 18a,b,c).

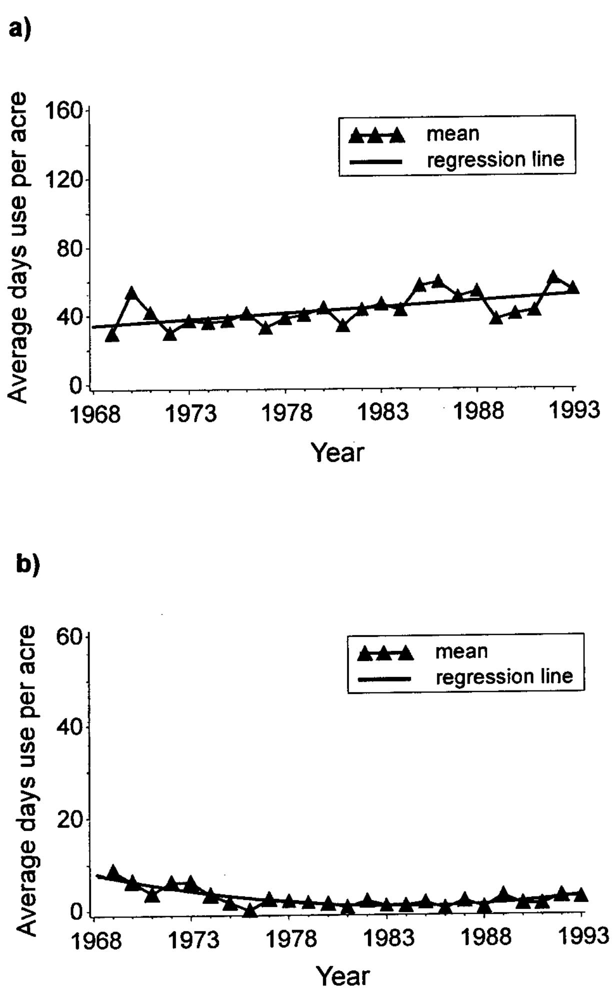


Fig. 6. Average days use per acre by elk (a), and mule deer (b) on grassland transects as determined by pellet count plots, 1968–1993.

Fig. 7. Average percent cover of bare ground (a), forbs (b), and mosses and lichens (c) on grassland transects, 1968–1988.

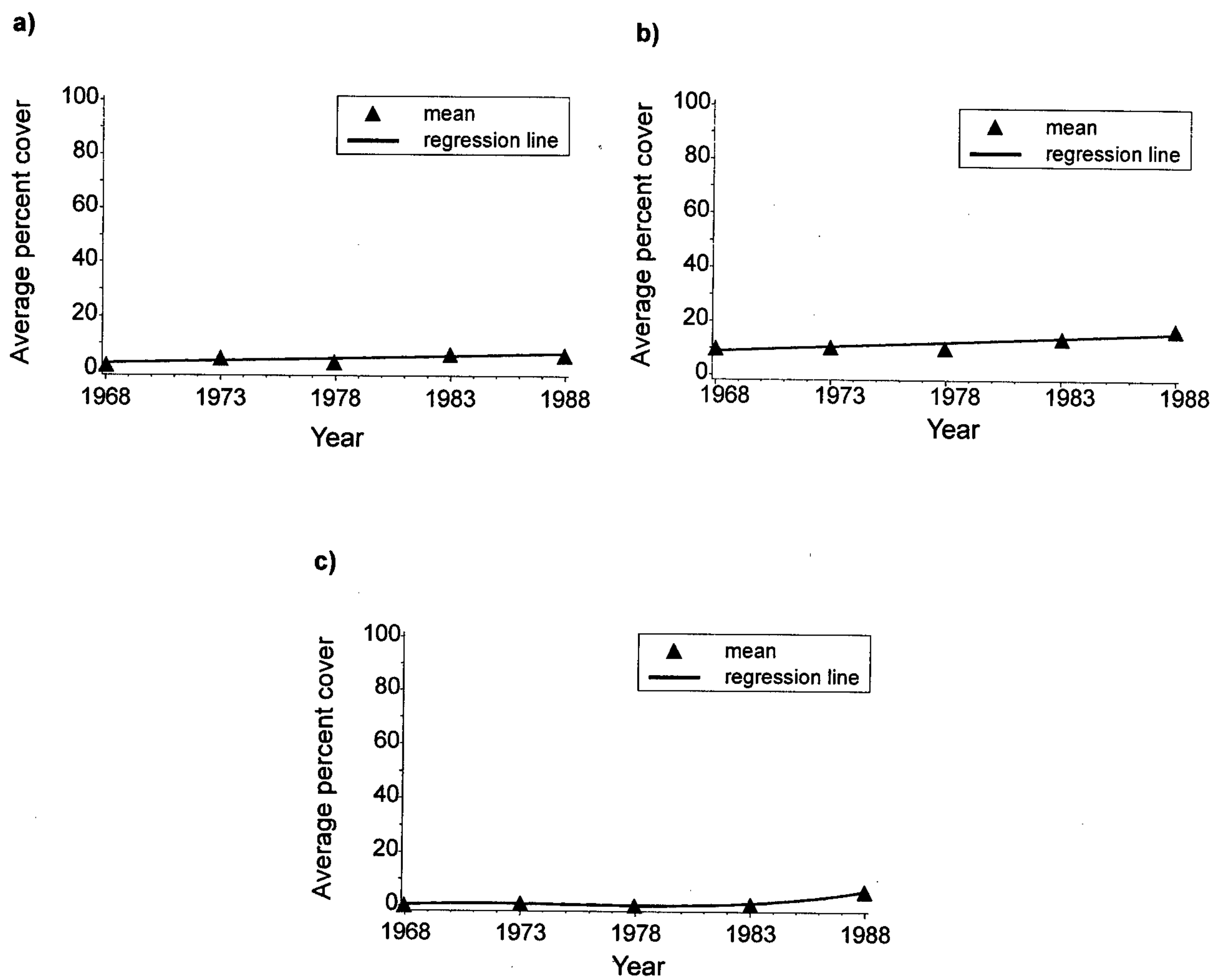


Fig. 8. Average percent cover of *Carex* spp. (a), *Selaginella densa* (b), and lichens (c) on grassland transects, 1968–1988.

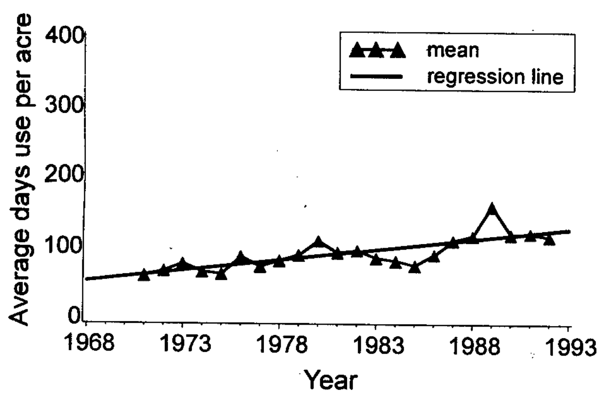


Fig. 9. Average days use per acre by elk on meadow transects, 1968–1992.

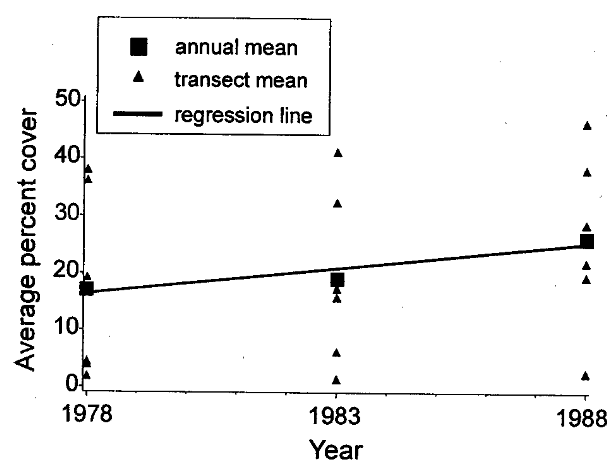


Fig. 10. Average percent cover of *Phleum pratense* on meadow transects, 1978–1988.

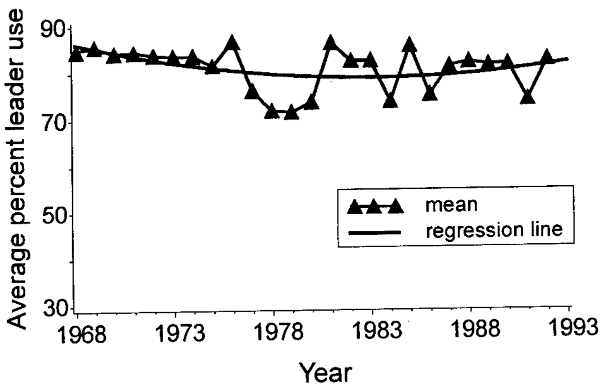


Fig. 11. Average percent leader use of *Salix* species, 1968–1992.

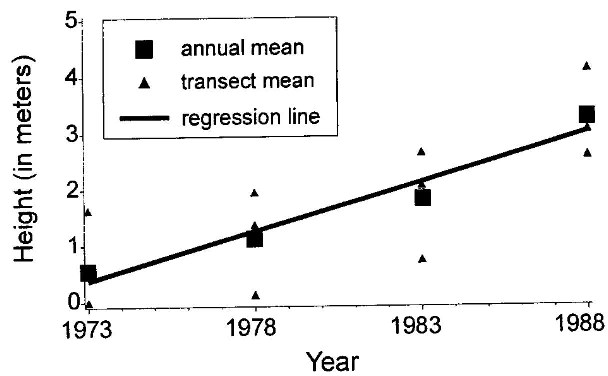


Fig. 12. Average height of *Alnus tenufolia* on willow transects, 1973–1988.

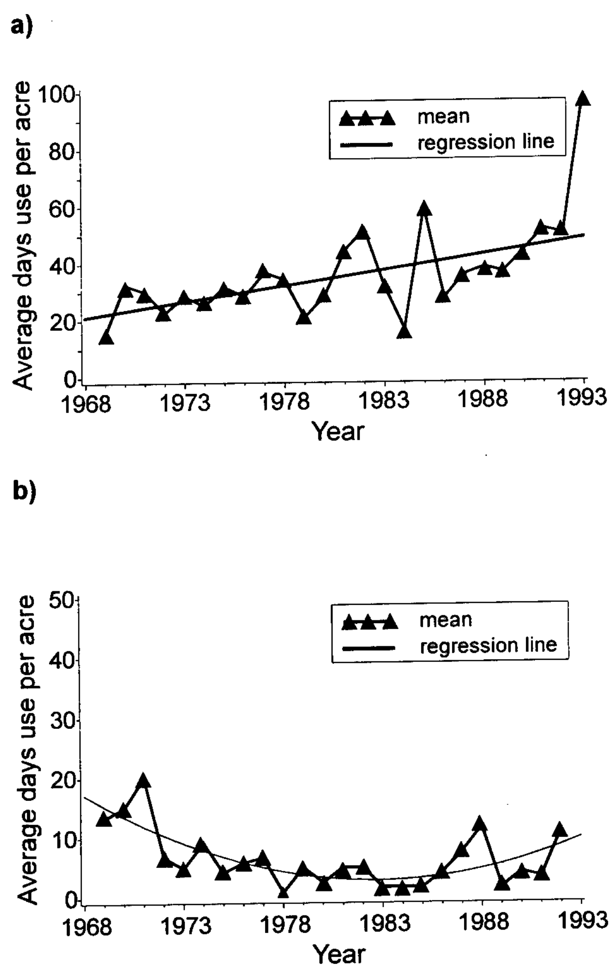


Fig. 13. Average days use per acre by elk (a), and mule deer (b) on sagebrush transects, 1968–1992.

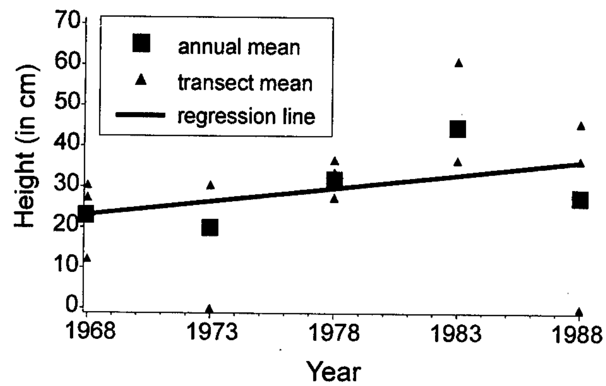


Fig. 14. Mean height of *Purshia tridentata* on sagebrush transects, 1968–1988.

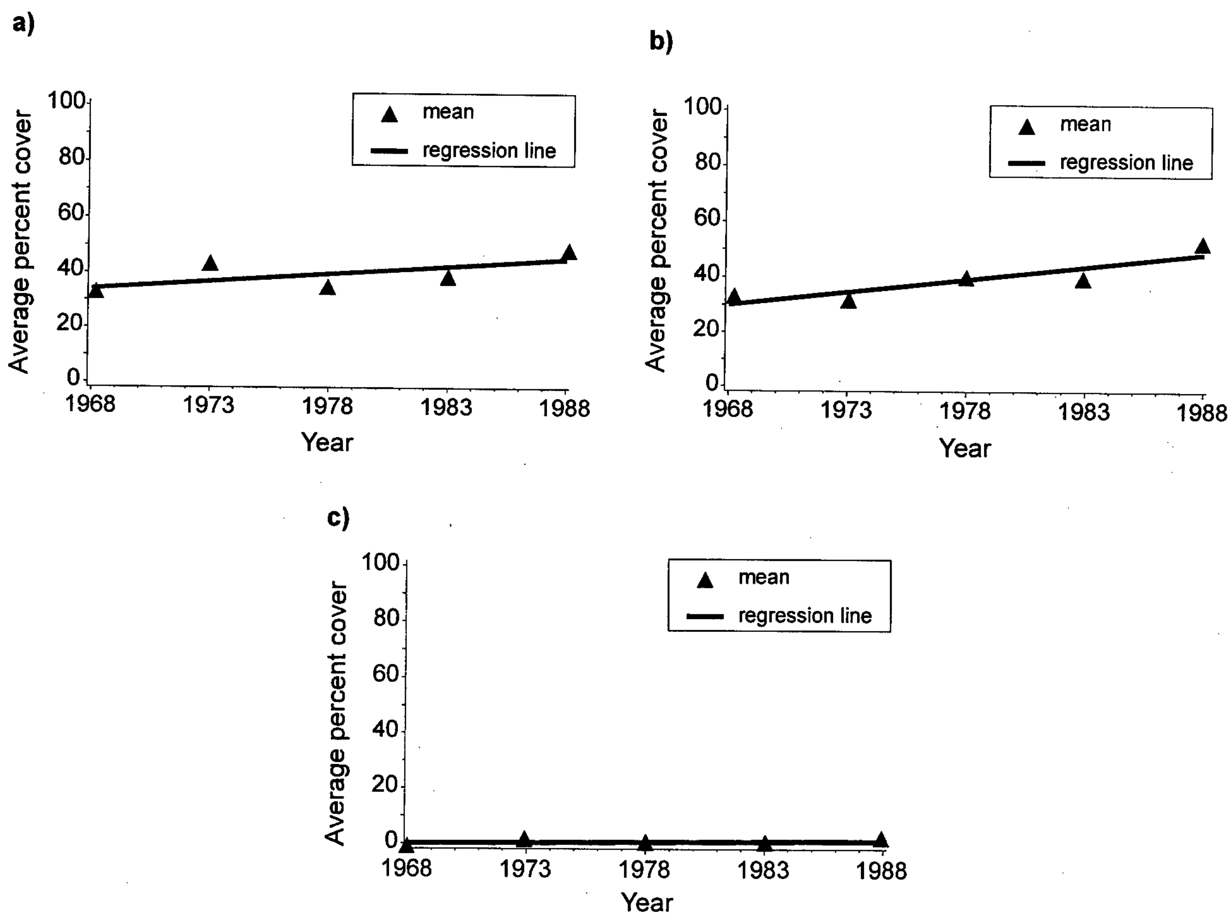


Fig. 15. Average percent cover of graminoids (a), litter (b), and mosses and lichens (c) on sagebrush transects, 1968–1988.

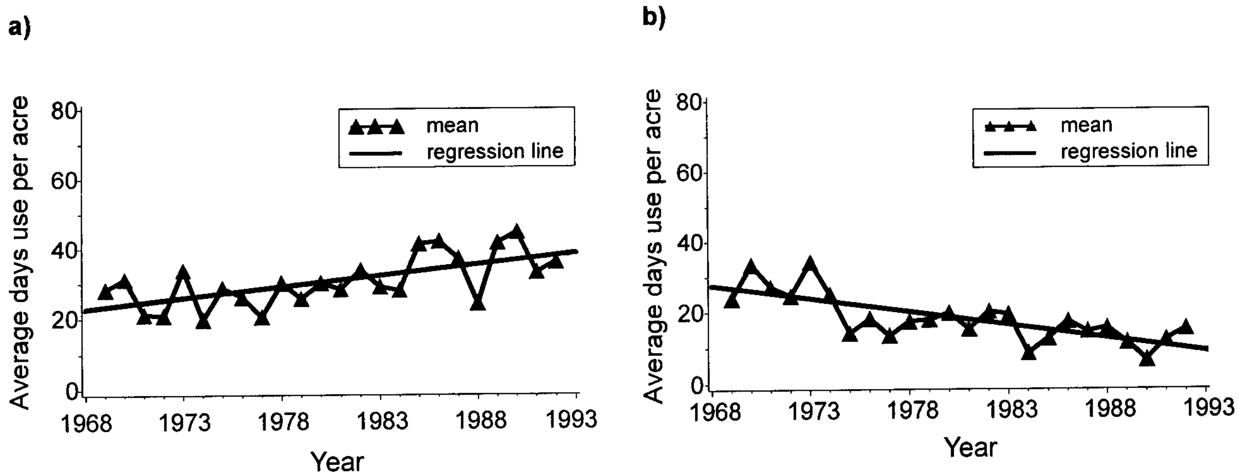


Fig. 16. Average days use per acre by elk (a), and mule deer (b) on bitterbrush transects as determined by pellet count plots, 1968–1992.

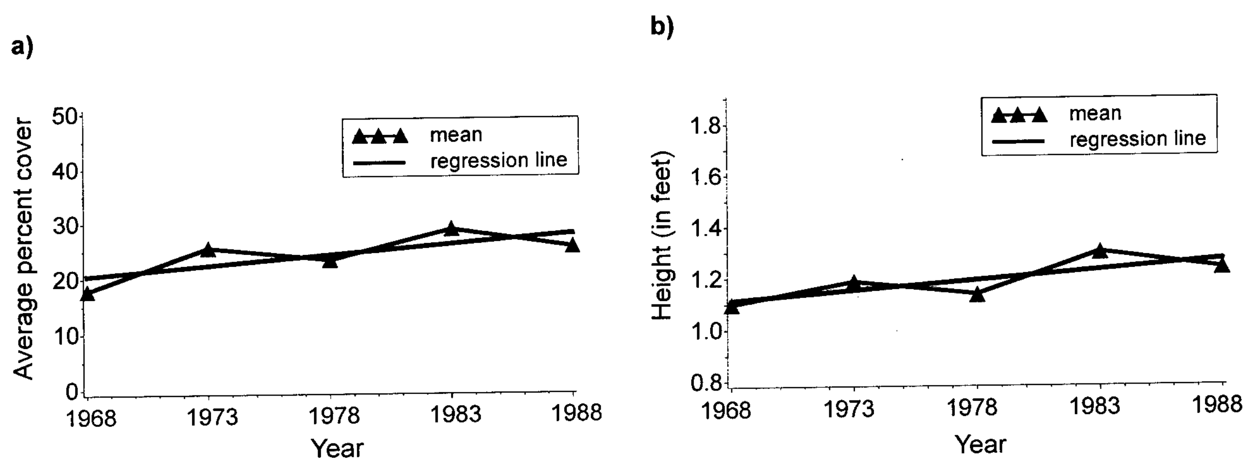


Fig. 17. Average percent cover (a), and mean height (b) of *Purshia tridentata* on bitterbrush transects, 1968–1988.

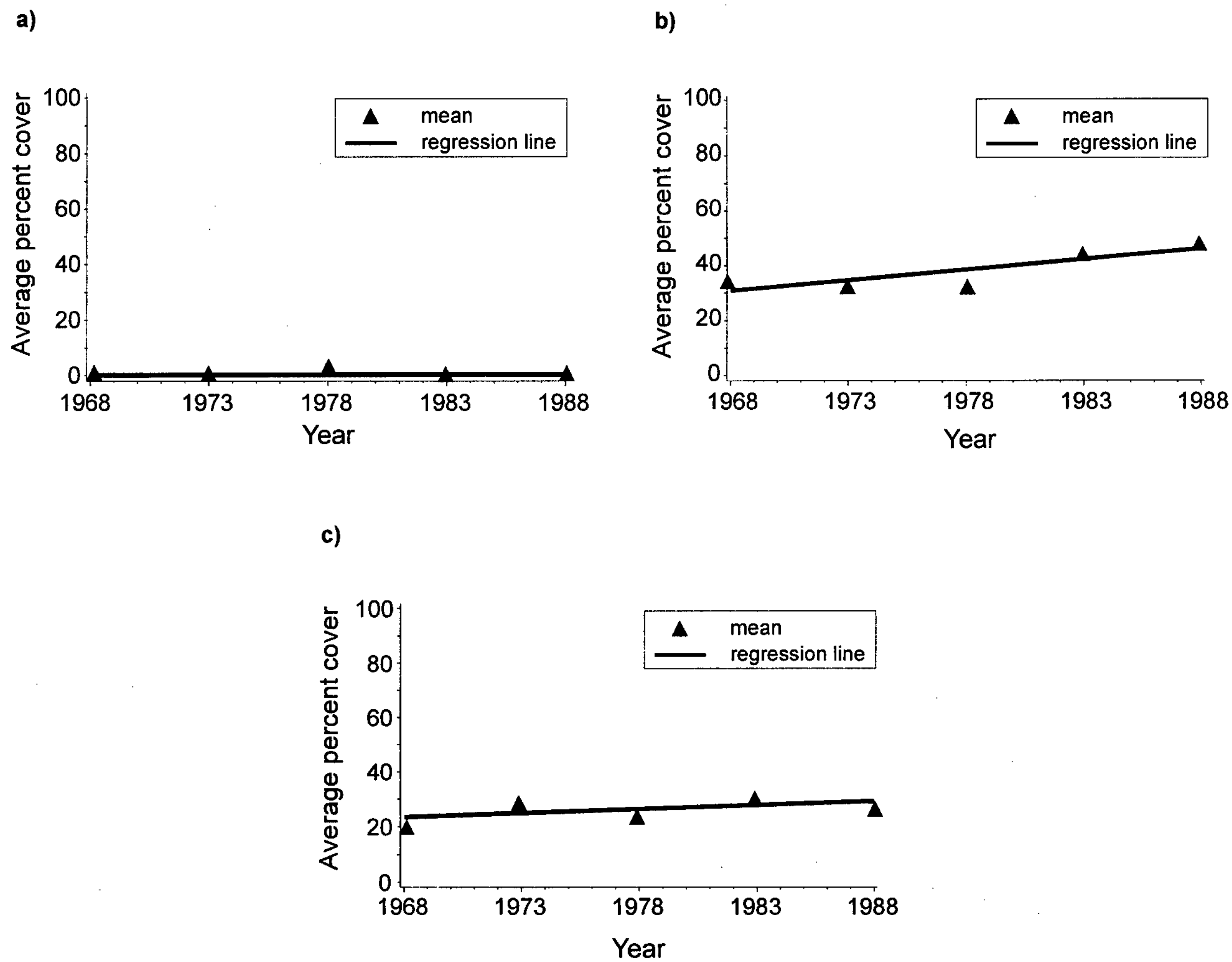


Fig. 18. Average percent cover of mosses and lichens (a), litter (b), and shrubs (c) on bitterbrush transects, 1968–1988.

Discussion

Vegetation Trends

We were unable to determine whether or not overgrazing occurred based on the experimental design and limitations of the sample. We concluded there were no overwhelmingly obvious indications of any overgrazing based on the following evidence: (1) bare ground increased only in grassland type and this increase, while statistically significant, was relatively minor, only about 4% (Fig. 7a), and there was no evidence of any concomitant reduction of plant cover; (2) no obvious significant shifts toward less palatable species were indicated; (3) assuming changes in plant productivity can be reflected by increasing canopy coverage, no decline, and possibly an increase in plant production, may be inferred from the increases in canopy cover of grasses and sedges; and (4) significant shifts in species composition, as would be indicated by significant increase of weedy species and exotics coupled with decreases of native plants, were not evident with two exceptions. The first exception that we observed was an increase in cover in grassland of lichens and *S. densa*, which tend to grow on rock and gravel substrates (Nelson 1992). Their increase may be a response to the minor increase in bare ground. MacCracken et al. (1983) found that the lichen, *Parmelia chlorochroa*, was significantly associated with bare ground and drier sites in Montana grassland and sagebrush vegetation. This lichen decreased in the absence of grazing. Increases in mosses/lichens were also

observed in sagebrush and bitterbrush types. Anderson et al. (1982) reported a 3-fold increase of lichen and moss cover in moderately to heavily grazed areas over areas with light grazing intensity. During and Willems (1986) found similar decreases in lichen and mosses with decreased grazing in Dutch chalk grasslands. Second, we documented an increase in timothy, an exotic grass, over the study period. Timothy is grazing-resistant, but is also a preferred elk forage. The changes documented are not suggestive of overgrazing. However, we were unable to investigate all of our stated criteria of overgrazing. In particular, the very limited data from controls (exclosed vegetation) did not permit us to determine which of these changes were due to elk herbivory alone. The very limited data from within the exclosures (statistical tests were not possible) indicated there were similar amounts of bare ground, and that *Carex* spp., *S. densa*, and lichens also increased in the controls. Thus, at this time, and based on this data set and sampling program, we found no overwhelmingly obvious indications of any severe overgrazing of the herbaceous species. We do suggest, however, that additional data be gathered.

Increases in height of bitterbrush may be due to decreasing days use per acre by deer in both bitterbrush and sagebrush plots. *P. tridentata* is a primary browse species for mule deer (*Odocoileus hemionus*) as well as elk in both sagebrush and bitterbrush types (Stevens 1980; Hobbs et al. 1981).

Increasing height of alder may be an indication of changes in dominant species in these sites. However, though significant, this increase was relatively minor (approximately 1 ft [30 cm] average height increase over 25 years). The increase was not paralleled by similar increasing cover of alder and decreasing cover of willow species. Increasing heights of alder may reflect the fact that alder is not as heavily browsed by elk as willow (personal observation) and could point to an eventual shift in species composition from willow to alder.

Stevens' annual reports (Stevens 1983–1992) indicate increases in decadence and decreases in reproduction of willows on willow transects — an observation which is not corroborated by our analysis of willow percent cover data on these transects. While it is true that percent cover of willows decreased on at least two of the transects, the other four transects remained stable or increased over the 25-year time span (Fig. 19). Also, we were not able to use data from transect 22 in our 25-year analysis because that transect was moved after the 1982 flood destroyed the original transect. Our analysis does indicate declines on transects 17 and 19, the same two transects that Stevens noted as declining; however, these declines are offset in our analysis by increases in cover on sites 16 and 20. In Stevens' reports, only the declines in transect 17 were attributed primarily to elk, while declines on transect 19 in Lower Moraine Park were attributed primarily to changes in hydrology and secondarily to elk herbivory. A larger sample size across all winter

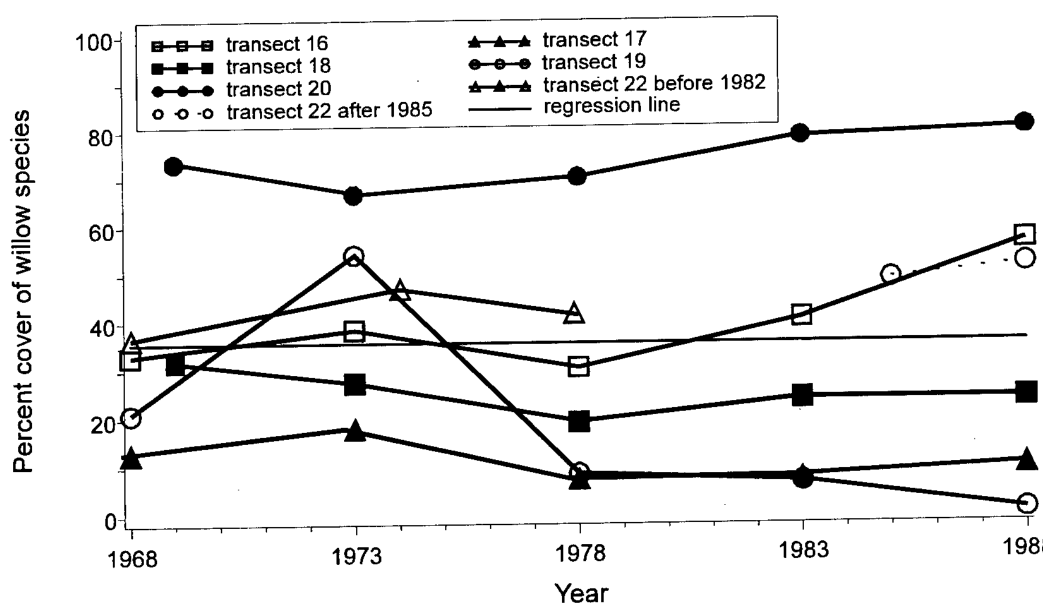


Fig. 19. Percent cover of *Salix* spp. by transect, 1968–1988.

range willow communities would give a better picture of the direction of change in these willow communities. Larger sample size would also reduce the impact of loss of a few sample plots to events such as the 1982 flood.

This same case is even more exaggerated in the aspen transects. Stevens' annual reports specifically mention declines in aspen recruitment (Stevens 1969–1992). Slight increases in the density of mature trees (>8 ft tall) were observed on all three transects (Fig. 20a). While the density of young trees declined dramatically on one transect, it increased on another, while it initially decreased, then increased again over time on the third (Fig. 20b). When all transects are analyzed together, the impact of dramatic change in one plot is diminished. With only three transects to analyze, we have no way of knowing whether any of these plots is more representative of conditions on the range as a whole than any other. That the plots were not randomly selected makes conclusions about the entire winter range aspen community even less valid. Addition of data points from a fourth transect illustrates how additional points might or might not cause shifts in averages for a community type (Fig. 20c,d). It should be pointed out that many of the aspen sampling points actually violated one of the assumptions necessary to use the point-centered quarter method (Mueller-Dombois and Ellenberg 1974). The point-centered quarter method is limited by the need for each quarter at a sampling point to contain a plant. Many points contained one or two quarters which had no aspen plants. Thus, the aspen densities reported here are not entirely accurate, and more suitable methods should be considered in future monitoring programs.

Increases in graminoids and litter in grasslands on the study area suggest that with increased elk herbivory grazing "lawns" may be developing (McNaughton 1984). One species of exotic grass, timothy, increased in meadow sites and native sedges increased in grassland sites. Both of these graminoid groups are grazing-resistant and potential increasers under elk grazing (Smith 1960). Both timothy and sedges are readily consumed by elk (Hobbs et al. 1981, 1982), and are not considered unpalatable forages to elk. Are the increases in timothy and sedges resulting in declines in other native species? Our data did not verify any declines, but we hasten to add that such declines might have occurred and not been detected with this sampling program, due to inadequacy in the number or extent of sampling.

Changes in species cover may be poorly estimated using cover classes of unequal sizes as occurred here. Methods which use unequal cover classes tend to overestimate abundance of species with low average cover and underestimate abundance of species with high average cover (Floyd and Anderson 1987; Mitchell et al. 1988). As a result, a minor change in canopy cover of a particular species may occur and be obscured since only the midpoint of the class is used in calculation of average canopy cover for the sites. For example, two coverage values, one of 52% and one of 74%, would both be assigned to the cover class 50%–75%, the midpoint of which is 62.5. Thus, the 22% increase in canopy cover of this species would not be evident. Canopy cover estimates may also be biased by size of individual plants of a species, plant density, or size of the plot being sampled (Hanley 1978; Floyd and Anderson 1987; Mitchell et al. 1988). Tests of statistical power to estimate the number of samples required to detect a treatment effect were not routinely done in 1968. Thus, either the degree of community stratification or the number of sample plots may have been inadequate to detect a significant trend even when one actually occurred.

Research and Monitoring Recommendations

A Clear Statement of Questions and Needs

No monitoring program can afford to sample everything, everywhere. Thus, research hypotheses need to be more clearly stated than in the past. The changes in vegetation and ecosystem parameters that will be acceptable need to be better defined. Any premise that a significant wintering population of elk will have no effect on vegetation or ecosystem processes is naive. Any human-caused concentrations of elk should be managed by the National Park Service (U.S. Department of the Interior, National Park Service 1988). At what point do elk concentrations become unnatural? At what point do vegetative conditions become unacceptable? These threshold points need to be unambiguously defined. Predictions need to be made as to what density of elk wintering in the park should be expected from a naturally functioning ecosystem. This will be a complex assignment because elk migrations are disrupted by human developments to some extent, and because so little information exists on prehistoric conditions. This subject is so complex that an advisory panel was asked to assist park staff in April 1997 on the development of vegetation management goals for elk range in the park.

In particular, park staff needs to decide which groups of plants or ecosystem processes to focus on. Should the focus be on plants which are most sensitive to changes in elk numbers? That would be most valuable if any control of elk numbers is proposed, or if there is an increase or decrease in elk numbers. This analysis suggests that timothy, sedges, lichens, *S. densa*, and bare ground are most sensitive to changes in elk numbers. Should rare or

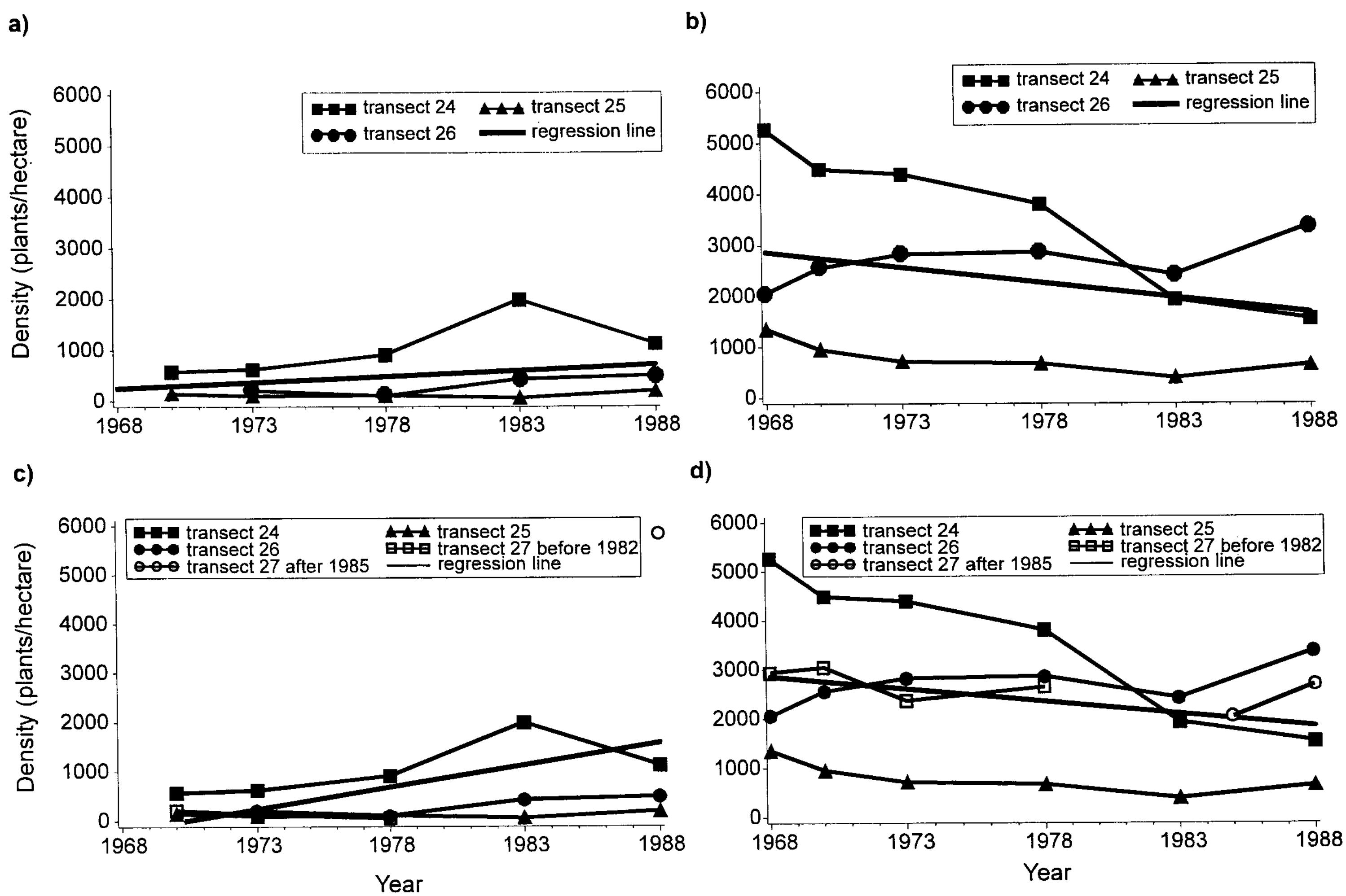


Fig. 20. Density of *Populus tremuloides* on aspen transects. Mature trees (over 2.44 m in height) with only three transects and regression line (a), and including transect destroyed by Lawn Lake flood (c). Young trees (less than 2.44 m in height) with three transects and regression line (b), and including transect destroyed by Lawn Lake flood (d).

declining plants be emphasized? If so, the ongoing studies of Stohlgren et al. (1997) should tell the park what species to focus on. Changes in rare plants will be harder to detect and will require more sampling and dollars. Another option is to focus sampling on highly visible or high public profile plants, such as willow and aspen.

Monitoring of Ungulate Populations

Ultimately, elk population goals will be set as a way of achieving vegetation goals. Thus, any continued monitoring of vegetation under current elk management, or any change in elk management, will depend on a parallel effort to census the elk population. Predictive modeling might be useful in this context. What level of change in elk density will result in a specified vegetation response? A census technique(s) is needed by park management that will detect a $\pm$15% change in elk numbers both in town and in the park sectors (Homer Rouse, Park Superintendent, 1993–1995, personal communication). One town census should be conducted per year. Census work in progress, employing the Idaho aerial sightability model (park sector) and mark-resight (town), meets these criteria. Detailed classifications (bulls, cows, spikes, calves) should be conducted each year to sample production and recruitment in the elk population. This should continue to be done both in town and the park. Any evaluation of density-dependence in the elk population will require annual counts and detailed classification to detect, for example, a decline in calf recruitment with increasing elk population size that might indicate density dependence. Since each year will provide only one data point in regression analyses, no annual counts/classifications should be missed.

Mule deer populations may have declined over the sample period. Additional monitoring of the mule deer population should occur.

Experimental Design

The single greatest strength of the 25-year sampling program and data set of Stevens (1980, 1992) was the high level of consistency in how and when the measures were taken (Stevens took every measure) and the impressive length of time of the study. Another strong point was that the samples were well-distributed over the entire winter range. Also, the transects were placed in areas of greatest elk use and densities. Thus, the sampling was most likely to detect any changes due to elk abundance. The sampling program was a tremendous accomplishment in its consistency and number of years, and we compliment Dave Stevens for the work.

Stevens' (1980, 1992) 25-year study provided an impressive data set which sampled a large number of variables and vegetation types. However, future experimental or monitoring programs would benefit from consideration of additional design features, including: random site selection stratified by vegetation type; larger numbers of independent sample sites; objective and quantitative measurement techniques; consistent data collection methods; and consistency of sampling dates within vegetation types (Table 3).

The single greatest weakness in the Stevens (1980, 1992) program was in the lack of adequate controls. Equal sampling effort should have been expended in control situations such as inside grazing exclosures or in similar sites with few elk. Otherwise, the treatment of elk grazing cannot be isolated from other potentially confounding influences such as effects of climate, fire suppression, natural succession, or others. For example, timothy might have increased both inside and outside of exclosures. We do not know that.

Only three large long-term exclosures exist and they were erected 6 years prior to the release of elk from controls and no canopy coverage data were collected

Table 3. Advantages and disadvantages of various experimental designs and sampling regimes.

Experimental design	Advantages	Disadvantages
Annual measurement	More data points in regressions	Greater monetary and labor cost
Less frequent measurements	Fewer data points	Lower monetary and labor cost
Greater replication at a site	Samples within-site variance Time efficient	Loss of landscape inference
Landscape replication	Greater inference	Time consuming
Random selection of sites	Greater inference	Greater monetary and labor cost
Representative site selection	Best when funds are limited	Less inference

within these exclosures at the time they were erected. These exclosures sample slightly different communities, only one of which is included in two different exclosures. The exclosures are inadequately replicated and all three are located within the Beaver Meadows area and therefore represent one small portion of the entire winter range. Sampling in these exclosures was inconsistent over the study period and not conducted in concert with the sampling of the unprotected vegetation transects. As a result, we were unable to do a trend analysis using these data. We did visually examine mean canopy coverage data for those species which showed significant changes on the unprotected vegetation transects, but the data were too limited for statistical tests (Appendix). Thus, our highest priority recommendation is that any new sampling program include the new network of exclosures that were established in 1994 and/or any additional exclosures added at a later date.

Additional limitations of the 25-year program were that the sample sites were originally selected to be representative and their selection was nonrandom. Greater inference can be made to the entire elk winter range if sample sites are located in a completely random fashion across the entire landscape. Representative site selection is the preferred option if the number of sample sites is very limited by funds. But when sites are selected nonrandomly in representative locales, statistical inferences are limited only to those plots themselves, and not to the general area, nor to the entire winter range. Nonrandom selection of sample sites limits conclusions about changes on larger scales.

Also, the 25-year program relied heavily on line transects. While use of line transects is a widely accepted and efficient means to sample plant communities, they have a high degree of spatial autocorrelation. As a result, individual samples along a transect are not independent from each other. Within-site variance is reduced, but at an expense of time and labor. We suggest that this time would be better used sampling a smaller number of plots/sites, but across more sites. A greater number of sites would provide a more accurate estimation of the true means of variables measured. The size and shape of plots used to count pellets (100 ft^2) and the plots used for sampling plant cover (20 x 50 cm) were adequate. Aerial plant cover, however, is a highly variable measure easily influenced by observer differences, wind at the time of sampling, and other variables. We suggest basal plant cover is less variable and a better measure. We also suggest that plant productivity, by species, is even better, since ultimately the productivity of the site is the final measure of the success of any elk management program.

The 25-year sampling program provides a unique and valuable long-term data set for assessing trends. The complete dropping of this program is a decision that must be weighed heavily and is beyond the purview of our research group. We have identified enough shortcomings in the program to recommend that the program no longer be conducted in its existing fashion. If portions of the existing program are to be maintained, power calculations need to be conducted, and, if necessary, additional sample sites need to be selected. An equivalent number of samples should be added inside of the new exclosures to provide adequate controls to the treatment of elk grazing. Only the most valid plots and measures should be continued. Any of the remaining measures or plots that are subjective should be dropped. All of the new sites should be randomly located. We suspect portions of the current program would need to be approximately tripled to meet these criteria. Park staff need to ask themselves if they are comfortable with the measures, the original selection of sites, and a significant increase in time and effort to stick with portions of the old program. Any dropping of the old program would have to be weighed against the loss of a unique, long-term sampling program.

Should the park management decide to develop an entirely new sampling program, we suggest the following steps. First, park staff needs to decide which plant groups to focus on: species most likely to change, rare species, or high profile-visible shrubs and trees (see Discussion above). Second, the specific treatments to be sampled need to be selected. Will fire, trend over time, changes in beaver abundance or water tables, climate, or other factors be incorporated into the design? What should the sensitivity to any change in elk density be? Will the program need to detect changes due to a 25%, 50%, or 100% change in elk numbers? Third, the study area of concern needs to be defined. Should the sampling focus only on the high elk use areas, to save time and money? Elk use may not be linear in habitats as numbers change, so perhaps less preferred types should also be sampled. Fourth, once these questions have been answered, the optimal sample plot size, shape, and sample measures can be selected, and tests of power conducted to determine adequate sample sizes to detect a treatment effect. Fifth, plot locations can then be located randomly using the park's geographic information system.

Plant recruitment and population turnover rates need to be sampled. In particular, concern exists for inadequate levels of seed production, seedling establishment, root sprouting, and recruitment or stand expansion in aspen and willows. Willow stands and aspen clones appear to be stationary or slowly declining. Greater consistency in tagging of browse plants in the future would allow measures of age-specific mortality. In Stevens' work, changes in individual plant identification made it difficult to follow decline of the plant population through time. This problem could be solved in the future by having stricter definitions of plant age categories and

discontinuing tag numbers of plants which die, and assigning previously unused numbers to replacement plants which are added at later dates. Percent protein (N) should be measured, along with additional nutrient concentrations and fibrous constituents, if estimation of nutritional-based ecological carrying capacity is to be used in elk management. Nutrient measures could also provide information to evaluate the sustainability of elk grazing in the system. Belowground plant reserves have been ignored, and although difficult to measure, they are important to understanding the effects of elk on plant production. Therefore, we recommend the park consider looking not only at traditional vegetation species composition, but also at these ecosystem variables. Ultimately, managers may determine that a shift in species composition is acceptable, providing the productivity and sustainability of the system is maintained.

Acknowledgments

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Appendix. Percent canopy cover of selected species from within three exclosures erected in 1962. Means (and standard errors) are reported. Means with no reported standard error indicate only one data point available for that sampling period.

Vegetation type	Species	Year 1970	1971	1975	1984	1990
Grassland	Bare ground	12.00 (6.00)	23.20 (0.30)	9.60 (3.60)	8.20 (1.90)	10.70 (5.55)
	Carex spp.	1.00	Trace	0.40 (0.30)	1.18 (0.72)	3.60 (2.50)
	Selaginella densa			0.90 (0.10)	0.89 (0.06)	1.05 (0.35)
	Lichen				2.14 (0.95)	1.25 (0.75)
Meadow	Bare ground	1.55 (1.45)	36.25 (5.15)	12.50 (2.50)		
	Carex spp.	45.50 (8.50)	0.55 (0.45)	2.00 (1.00)	21.20 (9.50)	14.90 (9.50)
	Selaginella densa			1.50 (0.50)		
Sagebrush	Bare ground	22.30 (2.33)	13.60 (3.15)	7.50	20.30 (3.60)	15.27 (1.29)
	Carex spp.	14.00 (6.03)	3.63 (0.88)	6.50	13.08 (2.34)	12.73 (1.65)
	Selaginella densa			7.00	0.88 (0.78)	0.90 (0.20)
	Lichen				5.85 (2.15)	1.80 (0.80)

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13. ABSTRACT (Maximum 200 words)

Little experimental information is available on the relationships between herbivory by native ungulates and vegetation in relatively undisturbed environments. A quasi-experimental situation exists in Rocky Mountain National Park, where elk (*Cervus elaphus)* populations have increased 3-fold since 1968 following their release from artificial controls within the park. We reviewed data collected on vegetation transects monitored over the 25-year period, 1968-1992. Data were subjected to rigorous statistical analysis to detect trends following the release of elk from artificial controls. Increases in elk habitat use and decreases in deer habitat use were observed. Significant increases in cover of mosses and lichens occurred in three of four vegetation types. Percent cover of bare ground, forbs (*Selaginella densa*) and Carex spp. increased on grassland transects. Increases in timothy (*Phleum pratense*) were observed on meadow transects. Graminoid and litter cover increased on sagebrush transects, and shrub cover and litter cover increased on bitterbrush transects.

Some grazing induced responses were detected. Grazing resistant species such as sedges (native), timothy (exotic), and club mosses increased and the amount of bare ground increased on some grazed sites. Theamount of bare ground increase was minor (34%), and grass and shrub cover increased in the shrub plots.

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